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EXPLANATION OF PLATE XXXII.

Shells of *Patella vulgata* L.

The actual lengths of the shells are as follows.—

1st Row.—7 mm., 8·9 mm., 10 mm., 11 mm., 13·5 mm., 15·4 mm., 17·2 mm.
2nd Row.—20·8 mm., 23 mm. (sexually mature), 26·6 mm. (about 12 months old), 30 mm. (15 months).
3rd Row.—33·3 mm., 38·5 mm. (over 2 years), 40·7 mm.
4th Row.—44·1 mm. (over 3 years), 47·3 mm. (about 4 years), 51·2 mm. (about 5 years).
5th Row.—53·5 mm., 61·2 mm. These two limpets are at least six years old, and may be more.

3. The Life-History of the Agrionid Dragonfly.

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(Plates XXXIII. & XXXIV.*)

Introduction.

So far as I have been able to find, the life-history of the Dragonfly has not, up to the present, been studied in detail by anyone. Various facts have been noted by different observers, but no one has apparently attempted to hatch the eggs and follow out the changes which take place during the larval or nymphal condition.

The general facts in the life-history are well known. The perfect insect lays its eggs in the water; after an unknown period there emerges from the egg a sub-aquatic creature known as a nymph, which grows, casting its skin at unknown intervals, and which finally crawls out of the water and dries itself in preparation for the final ecdysis.

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* For explanation of the Plates see p. 285.

In this paper I propose to describe the details of the development so far as I have been able to ascertain them; and, while so doing, I shall incorporate a few casual observations on the anatomy which have been made in the course of the work and from watching the living creatures themselves. Although incomplete, these observations are, I believe, accurate, and may prove of some use to those interested in the comparative anatomy of the Insecta.

I commenced studying the Dragonfly in 1903, at the Sutton Broad Laboratory; but it was not until July 1906 that I seriously undertook the investigation of the life-history. From the literature on the Odonata I was able to obtain but little assistance. Packard (1866) published a paper on the development of the Dragonfly *Diplax*; but that paper deals for the most part with embryology, and the illustration of the newly-hatched larva—which is reproduced by Dr. Sharp, (1895, p. 419),—although truly representing the first stage of the true nymph, does not represent the creature as it comes out of the egg. Brandt, Dufour, Amans, Gilson, and various others who have worked at the Odonata have dealt with their anatomy and physiology, but not with their life-history; and W. J. Lucas (1900), in his book on the British Dragonflies, only refers in a general way to the life-history. He also makes the mistake of regarding the first stage of the true nymph of *Sympetrum striolatum* as the form which emerges from the egg.

It was necessary therefore to start *de novo*, and for this purpose I endeavoured to collect some eggs from the dykes in the neighbourhood of the Laboratory. The females of all the Zygopteridæ, or thin-bodied dragonflies, like those of the Æschnidæ but unlike those of other Anisopterids such as Libellulidæ, Gomphidæ, &c., are possessed of an ovipositor and lay their eggs in the tissues of floating aquatic plants. They settle on a floating leaf of *Hydrocharis*, *Potamogeton*, *Anacharis*, &c., and dip the end of the abdomen into the water, often immersing the whole of it. According to some books, the females actually go under water at times when ovipositing; but I have never seen this. In the case of those plants with broad floating leaves, the apex of the abdomen is curved under the leaf so that the ovipositor, which is on the ventral side of the 9th abdominal segment, is brought into contact with the lower surface. The ovipositor consists of two equal lobes placed side by side, each with a sharp point projecting backward. The two halves of the ovipositor work together and pierce a small hole in the leaf-tissue. They then separate slightly from each other, and between them a single elongated egg passes down and becomes wedged in the hole in the leaf. Only one egg is buried in each hole. Some discrimination is exercised as to the piercing of the plant-tissues, as the ovipositor moves about over the surface before actually entering the leaf. The eggs are easily found in the thin leaves by holding these up to the light.

East Norfolk is rich in dragonflies*, not only in species but in individuals. A great number of females of *Agrion pulchellum* Lind., *Ischnura elegans* (Lind.), *Erythromma naias* (Hansen), *Lestes sponsa* (Hansen), and *Enallagma cyathigerum* (Charp.) were ovipositing at Sutton in the end of July. Eggs were therefore not difficult to find; but it was a somewhat laborious task to collect a large number, and, apart from this, it was impossible to know to which species any egg belonged or how long it had been laid. I therefore constructed a large cage, 15″ × 12″ × 12″, consisting of a wire frame covered with muslin, and this was placed over a large photographic developing-dish half filled with water. On the water I floated a few clean young leaves of the frog-bit (*Hydrocharis morsus-ranæ* L.) cut off from the plant, having first examined them carefully to make sure they contained no dragonfly eggs. I then captured six pairs of *Agrion pulchellum* Lind. and put them in the cage. It is extraordinary how dependent upon the direct sunlight is the vitality of these insects. On dull days, or when the cage was in the shade, the prisoners were in what appeared to be a torpid condition, clinging to the muslin sides of the cage and not moving for hours at a time; but on a bright day, or as soon as the cage was put into the sunlight, the scene became one of extraordinary activity: the males fighting one another for the females, and the combatants constantly falling into the water, from which, however, they always succeeded in escaping.

The peculiarity of the male reproductive organs—the vasa deferentia opening on the sternite of the 9th abdominal segment, while the organ of intromission is situated on that of the 2nd segment,—and the consequent peculiar method of transference of the spermatozoa to the female are apparently unique in the Odonata. I have never seen the actual transfer of the sperm to the sperm-sacs of the male, although in some individuals which have emerged in captivity I have noticed the tendency to curl the abdomen as if making attempts to bring the 9th and 2nd abdominal sternites into contact. Whether the sperm is transferred to the sacs once and for all, or whether the supply in the sacs is replenished from time to time, has apparently not been observed; but the female, at intervals in the process of oviposition, obtains further supplies of sperm from the male.

The male is furnished with claspers at the apex of the abdomen, by which he grips the notum of the prothorax of the female; and the pair fly about attached in this manner. The adaptation of these parts to one another is so close that only the claspers of the male of its own species can hold the prothorax of a female. Thus one very definite means of separating the females of *A. pulchellum* and *A. puella*, which very closely resemble each other, is the form of the notum of the prothorax, and I give drawings of this part of both these species. It will be seen that the males also differ somewhat in this respect, but to a less extent than the females.

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* See 'Victoria County History: Norfolk,' vol. i. (1901). Also, for Agrionidæ, "A Bionomical Investigation of the Norfolk Broads," Trans. Norfolk & Norwich Nat. Soc. vol. vii. (1904).

Either while a pair are flying about attached *per collem*, or while so resting, the female curves her abdomen underneath her in such a way as to bring the underside of her 9th segment into contact with that of the 2nd abdominal segment of the male; and the parts are so constructed that a firm attachment can take place, and the spermatozoa are transferred from the sperm-sacs of the male to the oviducts of the female.

After a contact of shorter or longer duration, from a few seconds to a minute or more, the female once more straightens herself out and sooner or later oviposition commences. This is most commonly done while the male is still holding the female *per collem*, but, though I believe less commonly, the female will oviposit without being held by the male. The male remains entirely passive during oviposition, apparently obeying the will of the female. When she flies, he also flies; but she directs, or seems to direct, the course. She seeks the aquatic vegetation and deposits her eggs as already explained. The male meanwhile rests either with his legs on the leaf or more commonly standing erect in the air, his body rigid, his legs folded, and himself supported only by the claspers attached to the prothorax of the female.

I kept the prisoners in the cage for about a week, feeding them on flies and other insects captured with the sweeping-net. The prey crawled about on the muslin, and the dragonflies, flying about in the cage, picked them off and either ate them while still flying or after settling on the sides. A large number of eggs were meanwhile deposited in the frog-bit leaves, besides very many which I found in the bottom of the dish. The eggs were laid during the first four days of August, and I placed the frog-bit leaves in tumblers of clean water and also collected a number of the loose eggs and dealt similarly with them.

After about a fortnight the leaves showed signs of decay; and towards the end of August nothing of them remained but a mass of decayed vegetation at the bottom of each of the tumblers, and my hopes of seeing any nymphs from the eggs vanished. However, on the 28th of the month numbers of nymphs appeared on the top of the mass of decay—almost four weeks after the deposition of the eggs. Although the majority of the eggs hatched at one time, nymphs were appearing for a fortnight or three weeks after that; and the same fact was noticed with the eggs of *Ischnura elegans* on another occasion.

The eggs which were dropped in the bottom of the dish never developed at all, and were all decomposing within 10 days. I have found that the eggs of the water-beetle *Dytiscus* also failed to hatch when cast loose instead of being buried in plant-tissues, as they normally are; and Miall (1895, p. 40) mentions that Lyonnet also found that loose eggs of *Dytiscus* never hatched.

It has occurred to me that this failure of loose eggs is due to asphyxiation, as possibly the eggs buried in the plant-tissues obtain a certain amount of air from the intercellular spaces of the plant; but if this is the case, it is somewhat surprising that the decaying leaves of the frog-bit retained sufficient air to supply a fair number of eggs.

At the time when the nymphs appeared I did not observe the emergence of the nymph from the egg; but I have since had the opportunity of watching nymphs of *Ischnura elegans* hatch, and I have no doubt, from the similarity in all the later stages, that the peculiar phenomena observed in the case of *I. elegans* occur in all the Agrionidæ, and, from the fact that I have observed some of the same phenomena in one of the Anisopterids, *Sympetrum striolatum*, they are evidently common to all the Odonata.

The dragonfly, both as a nymph and as an imago, requires living animals as food, and at the commencement of the work the difficulty was to find food small enough for the nymphs, which were but little over 1 mm. in body length. An infusion of horse-dung in water solved this difficulty, as in a few days it swarmed with life, one jar in particular constantly producing, for five or six months, a rich supply of *Paramœcia*, which the nymphs ate readily. As the nymphs grew the *Paramœcia* were replaced by daphnids, and it was surprising what large specimens the nymphs caught and demolished. Daphnids served as food all through the nymph stage after the protozoa became insufficient.

The nymphs proved exceedingly easy to rear. A number of them, as soon as they appeared, were sorted out and measured, and each was then placed in a tumbler of water by itself, a small piece of *Anacharis* being put in to give it foothold and also to keep the water fresh. Each tumbler was then labelled, and a record kept of the life of its occupant. The water in the tumblers was only very occasionally changed, and only when the glass became so thickly coated with algæ that I could not see the inmate. For the first two months of their life the nymphs were examined and measured under the microscope at least twice a week—for the first week or two, every other day; but such frequent interference with their existence proved unnecessary, and latterly the examination and measurement was much less frequent, being almost entirely confined to the times of moulting.

Although I have only followed *Agrion pulchellum* and *Ischnura elegans* right through from the egg to the imago, I have also kept through many stages nymphs of *Pyrrhosoma nymphula* and *Erythromma naias*, and from my observations I think there is no doubt that, so far as the general facts go, what is true for one of these species is true for all the others.

In this paper I am treating the subject from two points of view. First, I have detailed the phenomena observed in relation to the stages in the life-history in which they occurred, the stages being marked by the successive moults. I have then gone into some detail with regard to the development of the form of the nymph—that is, morphologically rather than anatomically; and in this part of the subject one or two interesting facts as to the manner of growth of the external parts have been observed. This detail has brought to light a certain want of agreement between the stages as marked by the moults and the stages in the development of these external parts; and I have therefore, in conclusion, reviewed the question from the point of view of the significance of the moult. This latter part of the paper is very incomplete, since, although a number of facts on the subject of the moult in insects are known, there is insufficient material at present upon which to base any really satisfactory theory. However, this is merely forestalling the conclusion.

THE PRONYMPH.

The Agrionid egg is an elongated body, rounded at one end and bluntly pointed at the other, the point being a small pedicel. In *Agrion pulchellum* and *Ischnura elegans* its length is about 1·3 mm., but the size no doubt varies in the different species. The egg is inserted, as already explained, in the soft tissues of aquatic plants, the pedicel end being the last to leave the oviduct and being therefore nearer to the surface of the leaf in which the egg is deposited.

The period of incubation varies somewhat in length according to temperature, apart from the fact that all the eggs of a batch do not hatch on the same day. Eggs laid in the beginning of August took just less than four weeks before the bulk of them hatched, while eggs laid later in the year did not hatch for more than five weeks.

For some time previous to hatching the position of the nymph within the shell is easily made out. The head lies at the pedicel end of the egg, the antennæ, first maxillæ, and labium being directed backward on the ventral side of it. The first and second pairs of legs lie straight out along the ventral side of the abdomen, while the third pair are bent on themselves at about the junction of the tibiæ and tarsi, the latter lying forward below the tibiæ. The posterior abdominal segments curve round in the shell ventrally, the 10th occupying the rounded end of the shell. The caudal lamellæ lie forward along the ventral side, between the legs and the shell.

For at least three days before the egg is ready to hatch the heart can be seen beating, at first slowly but getting faster as the time approaches for the emergence of the pronymph. The posterior end of the heart is the part which develops and pulsates first, and although in the free nymph this is in the 9th abdominal segment, in the egg it appears to lie in the 10th segment.

The first sign of the approaching emergence of the pronymph is the cracking of the shell immediately beneath the pedicel. At this time the heart is beating vigorously, at about 100 pulsations per minute. The pedicel is then seen to be slightly removed from the egg, owing to the bulging out from the egg of an extremely fine membrane which is evidently extended with fluid. This membrane continues to expand until there is a gap of about ·15 mm. or even more between the pedicel and the rest of the shell. It is noticeable also that the pedicel is not carried up in a line with the axis of the egg, but rather dorsally to the axis, and although this process was only watched in two or three cases I believe that the direction of expansion of the membrane is perfectly definite.

This carrying up of the pedicel and the formation of the vesicle occupies one or more hours, and except for some occasional slight writhing movements of the gut and of the abdominal segments within the shell no other change is noticeable during that time. The vesicle is, in fact, formed many hours before the pronymph begins to emerge. Some time after the formation of the vesicle a pulsating organ appears in the head in the region of the mouth; and one or two hours after this organ begins to pulsate, the head of the pronymph begins to expand into the vesicle. It takes the shape of the passage, losing all semblance of a head, and slowly fills the vesicle until it once more touches the pedicel. All this time the pulsating organ continues to beat at about 28 beats per minute.

As the head begins to enter the vesicle the walls of the latter bulge slightly, showing that they are extended by fluid which is being compressed by the head. Almost as soon as the head completely occupies the vesicle the membrane bursts along the dorsal edge of the pedicel and the enclosed pronymph slowly comes out. Just previous to this body-movements are more noticeable, and the tenth abdominal segment moves round so as to be in line with the others; but until the membrane bursts, no part of the shell is unoccupied.

The pronymph appears to flow out of the shell at the start, but almost immediately it exerts itself and wriggles from side to side. It comes out in exactly the position in which it has lain in the shell; the lamellæ, bent under the body, coming out points first. The lamellæ straighten out more or less once the larva is clear of the shell, but the legs and mouth-parts remain outstretched and directed backwards.

From the moment of its escape the pronymph—a helpless cripple—shows active writhing movements, and within two or three minutes the skin on the back of the thorax splits along the median line and a moult takes place. The posterior abdominal segments contract and expand and gradually creep up inside the pronymph skin, drawing the lamellæ out of their sheaths. As the abdominal segments press forward, the thorax becomes arched up and the head bent down. The pressure in the dorsal region of the thorax ruptures the skin along the median line, and the thorax rises up through the split. In doing so it ruptures the skin further forward, and the head with the antennæ and mouth-parts is drawn backward and upward out of the old skin and all these parts at once assume their normal position—the antennæ pointing forwards, the labium doubling on itself and taking up its position below the mouth, the maxillæ likewise bending forwards and coming to lie on either side of the mouth immediately below the jaws. Further writhing of the abdominal segments forces the body still further out of the skin, and the legs are withdrawn from their sheaths. Once the legs are free, a final struggle clears the nymph of the pronymph skin. This latter is exceedingly thin and transparent, and almost invisible even under the microscope except for the fact that on each side of it is an irregular band of backwardly-turned projecting points. These lie scattered on either side of the thoracic and abdominal segments, but there is none on the head. These points are no doubt of use in assisting the pronymph to escape from the egg.

Owing to scarcity of material after the discovery of the above details of the pronymph stage, I was able to observe the emergence from the egg only in two or three cases, and I had not therefore opportunity of making many observations on the pulsating organ already referred to. Several points were, however, noted. The organ is not far from the position of the mouth; it contracts from in front backwards, apparently driving blood, since the corpuscles were visible, posteriorly, and the pulsation and direction of the flow were quite distinct. The drive was towards the dorsal surface near the posterior margin of the head, and a blood-vessel in that region (the aorta ?) could be seen showing slight bulging each time the liquid was forced to it. Blood could also be seen passing from the anterior part of the head back to the pulsating organ; but at times this flow ceased and the corpuscles appeared to oscillate backwards and forwards at each beat of the organ, just as they may often be seen to do in the ordinary blood-spaces of the body.

I could find no trace of a pulsating organ in the pronymph after it had escaped from the egg; but this might have been due to the fact that the creature was in constant movement for the two or three minutes of its existence. There is apparently no such organ in the nymph. If it only appears, as I believe, after the formation of the vesicle and disappears or ceases to pulsate as soon as the pronymph escapes from the egg, the obvious inference is that it has something to do with the emergence of the pronymph, and is, in fact, an embryonic organ. It is interesting in this connection that Wheeler (1893) has described an embryonic "subœsophageal organ" as occurring in insects, of which he says the cells somewhat resemble those of the fat-body. He places it in the tritocerebral segment of the head, and says that it disintegrates in the larva.

The function of the pulsating organ in the head of the Agrionid embryo seems to be to absorb the fluid in the vesicle, so as to allow the head to pass into it; but how it can do so is at present a mystery. In the embryo of the water-beetle (*Hydrobius fuscipes* L.) I find that there is a cephalic pulsating organ which becomes active a few hours before the escape of the embryo from the egg, and that during its activity the embryo enlarges so as to completely fill the egg. There is, however, no vesicle formed, and in that case I am almost certain the pulsating organ is not a special structure but merely a pharyngeal pump, which is found in the larva after its emergence and is similar to that in all suctorial insects. In the Agrionid nymph, however, there is no suctorial apparatus; apart from which, the blood-corpuscles visible in the pulsating organ oppose the idea that it is part of the alimentary canal.

Circulatory pumps, accessory to the heart, have already been described in insects, but so far, I believe, they have only been observed in imagines and larvæ and not as embryonic organs. Behn (1835) first discovered them in the legs of various Hemiptera, and Selvatico (1887), Pawlowa (1895), and others have described them in the heads of certain Lepidoptera and Orthoptera. Selvatico describes an enlargement at the anterior end of the aorta—the "frontal sac," a description which might possibly suit the organ in the Agrionid embryo.

The reversal of the blood-stream observed in the embryo is also not unique*, as Bataillon (1893) observed the same phenomenon in the pupa of the silkworm.

With regard to the formation of the vesicle, it is possible that it is due to the displacement of the fluid which presumably surrounds the embryo within the shell, or possibly the fluid is extruded from the embryo to be later reabsorbed.

Much, however, remains to be discovered with regard to these phenomena in the egg.

The Nymph. *Stage* 1.

The nymph which escapes from the pronymph skin is no longer than the pronymph, in fact the total length—not including the caudal lamellæ—is just about that of the egg from which it came. It consists of a head, 3 thoracic and 10 abdominal segments, and is an excellent example of the campodeiform larva. The head bears two antennæ, each of which consists of 3 segments, two basal ones, which are of characteristic form and except in size do not show any change during the life of the nymph, and a long bluntly pointed, slightly incurved apical one. Not far from its apex, and on its outer side, this apical segment bears a very small spur. The length of this segment is equal to about 70 per cent. of the whole antenna.

The mouth-parts consist of a pair of jaws of the usual

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* I have recently observed a reversal of the blood-stream in the heart of a well-grown nymph, and I imagine the blood was also passing into the last chamber of the heart by the last pair of ostea. It was escaping by the ostea in the 8th abdominal segment.

"mandibulate" type, a pair of maxillæ, and a labium of very special form usually known as "the mask." It is in shape more or less an isosceles triangle, the apex being turned posteriorly and lying, when in a state of rest, underneath the first thoracic segment. The base of the triangle is presented forwards and at each of the anterior corners is attached an appendage representing a labial palpus, which again is rather triangular in shape, being flattened above and below and having three sides, one of which is anterior. At its outer anterior extremity each palp bears a movable claw, and along its anterior border each palp is beset with four or five teeth, the innermost being much the largest and slightly curved inwards. The inner border of each palp is serrated, the teeth being small and curved slightly backward. The anterior border of the labium itself is also slightly serrated *, and when the mask is not in use the palpi lie against this border in such a way that the anterior edges of the two interlock, the movable claws overlapping. On the upper side of each palpus, attached near its outer border and not far behind the movable claw, is a single long incurved hair or bristle.

The thoracic segments bear each a pair of legs, but at this stage there is no trace of the wings nor are the pleural ridges present. Except for the possession of the legs there is nothing in outward appearance to distinguish the thoracic from the abdominal segments. These latter are also very similar to one another, except that the body tapers slightly towards the posterior end. The tenth segment bears the three caudal lamellæ, one median situated above the anus and two laterals, one on either side of the anus. The two main tracheæ, which pass along each side of the thorax and abdomen, curve inward and upward in the tenth segment and run out side by side in the middle lamella. At the points where they curve upward a single branch continues as a fine tube into the lateral lamella of its own side. The lamellæ at this stage are tubular, perhaps slightly triangular in transverse section, tapering to their apices and ending in a fine long hair; they bear along two or three lines a series of small hairs and in *Agrion pulchellum* they contain two patches of pigment, one near the apex and one about halfway from the base.

The transparency of the nymph at this stage enables one to see fairly well the internal organs. The gut consists of a pharynx leading to an œsophagus which opens out into a large thin-walled sac—which is apparently contractile—occupying the thoracic segments. At the posterior end of this sac there is a constriction, and immediately behind this is another large thin-walled sac which occupies most of the first six abdominal segments. This sac—the mid gut—is constricted posteriorly and opens into a small globular contractile portion of the intestine, in the anterior end of which open two Malpighian tubules, one on either side and

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* The serration does not appear on either the palpi or the labium until a later stage. Only faint traces of it are visible at this stage.

slightly dorsally. The rectum is the continuation of the small intestine and occupies almost the whole of the last four segments of the body. The small intestine at one time appears globular and at another as a thick cord of tissue, the contractions apparently commencing anteriorly and passing backwards. A contraction begun in the small intestine continues through the rectum, which, like the former, is sometimes a large sac and sometimes a thick cord. With regard to the number of Malphigian tubules, Wheeler (1891–3) suggests that the embryonic number in the Odonata "will probably be found to be 4 or 6." There are, however, only two in *Agrion pulchellum* at this stage.

The heart consists of nine compartments and lies in the abdominal segments 1 to 9. Each compartment is separated from the next by a pair of very distinct valves, which lie in the posterior region of each abdominal segment. Immediately in front of each pair of valves is a pair of ostia in the lateral walls of the heart, so arranged that when the valves are open between two compartments the ostia are closed. The heart opens anteriorly into the dorsal vessel, or aorta, which has only a slight contractile power, and this vessel runs forward into the anterior region of the head, where the blood-stream divides into two and passes downwards in front of the head.

There is at this stage no circulation in the antennæ or in the limbs. The blood returns through the body by various lacunæ. The two large lateral sinuses, in which at later stages the blood-flow is easily seen, are but little developed at present. The corpuscles, which are large more or less oat-shaped bodies, can be seen passing backwards along the "pericardium," and a few can be seen every now and again making their way up from the lateral sinuses and after much oscillation entering the heart by some of the anterior ostia. The great majority of the corpuscles, however, re-enter the heart by the two large ostia situated at the posterior end of the 9th segment. Between these two ostia is a strong ligament passing back into the 10th segment.

The ventral nervous system, so far as it is visible in the living nymph, consists of a large (double) ganglion in each of the abdominal segments 1 to 7, and between the ganglia the cord is double, the two parts being quite separate. Behind segment 7 these two cords pass backwards and break up into finer nerves.

There is no sign at this stage of any sexual armature. This first appears, I believe, about the 7th stage, but I have made very few observations on this point.

Stage 2.

At the first moult of the true nymph certain changes are visible, showing an advance in organization. The antennæ are now composed of 4 segments, the apical one having divided transversely into two of almost equal length. The labial palpi now each bear two long stiff incurved hairs, the second hair having appeared below the first at the same distance from the external edge of the palp and much nearer the base.

The lamellæ show no change in shape, but the two lateral ones now possess two tracheal tubes, the main branch as its enters the base having given off a smaller branch which runs up the lamellæ parallel with the main one.

In some specimens at this stage circulation of the blood is visible in the basal segments of the third pair of legs, but, as a rule, there appeared to be no difference in this respect between this stage and the previous one.

Stage 3.

The antennæ now consist of 5 segments, the third from the base having divided, cutting off about one-third of its length at the distal end to produce the new segment.

No change takes place in the labial palpi, but one pair of long stiff hairs has appeared on the upper surface of the labium itself. These hairs are situated nearer the anterior than the posterior end and are on each side of the median line fairly wide apart. They are directed forwards and, when the labium is at rest below the head, are immediately behind the mouth of the nymph.

The lamellæ are slightly wider vertically than before, but it will be necessary to deal with their development separately, as their changes apparently correspond with the rate of growth of the nymph rather than with the stage in its life-history.

At this stage there seems to be usually, if not always, circulation of the blood in the bases of the legs, but there is still none in the antennæ or in the lamellæ. I am not certain as to when circulation begins in these latter organs, but it appears to be established about the 6th or 7th stage, if not earlier. One interesting point concerning it is that it is apparently intermittent, as there are times when it is impossible to see any corpuscles moving, while at other times the flow is distinct and rapid. The circulation in these organs seems to be confined to the region round the main tracheal trunks, there being in each lamella a blood-space above and below these tracheæ. The direction of the flow in these blood-spaces seems to be reversible, as at times the blood may be seen flowing outwards above the trachea and inwards below, while at other times the opposite is the case. The circulation in the middle lamella also is sometimes the opposite of what it is in the lateral ones. At times the corpuscles oscillate backwards and forwards on both sides of the tracheal trunks. I shall have more to say concerning the lamellæ when I come to discuss the moults.

In one individual examined at this stage there were three Malphigian tubules.

Stage 4.

At the third moult no increase takes place in the number of segments of the antennæ. In the labium the labial palpi now each bear 3 hairs, the new ones having been added below the second. A second pair of hairs has also appeared on the body of the labium between the other two hairs. These new hairs may be as large as the first pair or they may be smaller, only attaining full size at the next moult. In later stages the new hairs always appear as minute spines and are often only half their full size after the following moult, although they are more usually full size by that time.

A marked increase in the extent of the circulation is now visible. The corpuscles can be seen passing up the inner side of the first, second, and part of the third antennal segments. About halfway up the latter segment they cross over to the outside of the antenna and return to the head. Circulation is also distinctly visible in the bases of the legs as far as the trochanters, passing out from the body anteriorly and back to the body along the posterior side and beneath the tracheal tube.

In the femora an irregular movement of blood-corpuscles is recognizable, but very few seem to be present and these are constantly being temporarily held up among the muscle-fibres.

Usually, in this stage, small ridges appear on either side of the second and third thoracic segments, this being the first trace of wing-development. The appearance of these ridges is not, however, always in stage 4. In a few instances I have noticed them in the previous stage, while in many cases they do not appear until the fifth stage, but either stage 4 or 5 seems to be the normal one for their appearance. The development of the wings, like that of the lamellæ, seems more closely connected with body-growth than with the moults. This statement, however, requires some qualification, for, although it is not possible to describe any definite condition of wing-development as being connected with any particular moult, there seem to be one or two very definite stages correlated with the approach of the final ecdysis. This will, however, be referred to later.

Stage 5.

A further increase in the number of antennal segments takes place at the fourth moult, the third segment from the base again dividing into two equal parts. This 6-segmented condition of the antennæ continues through the next four stages, in fact, until the commencement of the final nymphal stage is reached, when a change takes place.

The condition of the labium remains the same as in the previous stage.

Although no regular record has been kept of the rate of increase in the number of Malpighian tubercles, one nymph examined in the fifth stage had either 5 or 6 of these. The rate of increase in the number of these must become more rapid later on, as Schindler (1878) describes 50 or 60 as being present in the imago of *Agrion puella*.

Stages 6, 7, 8, *and* 9.

The labium in stage 6 usually has 4 hairs on each palp and three pairs on the labium. Each new pair of hairs as it appears on the labium arises between the original hairs, so that gradually the series takes the form of a crescent with the ends curving forwards stretched across the labium. In stage 7 the condition of the labium is usually the same as in stage 6.

In stage 8 the labium may be just as in the previous stage, but often, perhaps more usually, either a pair of new hairs has appeared in the crescent or one hair only has appeared, so that there are 4 hairs on one side and 3 on the other. I noticed this irregularity in a number of cases, and although such uneven developments occur in other stages they do not seem to be so common as in this one. Occasionally there are 5 hairs on each of the palpi. In stage 9 there seem to be, with scarcely any exception, 5 hairs on each palp and 4 pairs on the labium.

Stage 10.

This may be the final stage in the life of the nymph. The antennæ, if this is the final stage, will be seen to possess 7 segments, the additional one having been produced by the division of the 6th immediately above the small spur already referred to. I am not certain that this division takes place in all the Agrionidæ, but the statement holds good for *Agrion pulchellum* and *puella*,. *Pyrrhosoma nymphula*, and *Ischnura elegans*. I think that the nymph of *Erythromma naias* has antennæ of only 6 segments in its final stage, but I can only find notes as to one specimen of this species. Similarly, with regard to *Enallagma cyathigerum*, the only specimen of which I have kept a record had 6-segmented antennæ in its final stage. When this is the final stage of the nymph, the labial palpi usually possess 6 hairs each, while the body of the labium has a crescent of 10 hairs more or less evenly spaced and all pointing forwards. In other cases, however, the labium may remain as in stage 9 or there may be an intermediate condition, 5 hairs on each palp and 5 pairs on the labium itself.

The blood-circulation in nymphs in the later stages is, in the legs, apparently the same as described for stage 4. Bowerbank (1833, p. 243) describes the blood as circulating in the leg of *Agrion* "even to the very extremity of the tarsus, where, as in the antennæ, the particles of the blood are seen to descend on the one side of the leg and turning the extreme point to return up the contrary side to the one by which they came down." Even in the full-grown nymph I cannot detect a regular circulation beyond the trochanters, where the corpuscles can be distinctly seen passing from the anterior to the posterior side and returning to the body. This circulation is rapid—as rapid as in the abdominal segments,—but that in the tibiæ and tarsi is extremely slow and irregular, the few visible corpuscles being constantly held up for quite long periods.

In the antennæ the circulation extends now to the apex of the 5th segment. A few corpuscles can be seen travelling up the inner side very irregularly, there being constant delays and short rushes. At the apex of the 5th segment they quickly pass over to the outer side and travel back to the head in the same easy stages.

Bowerbank (*l. c.*) mentions that the nymph he examined had antennæ of 6 segments and that the circulation only extended to the extremity of the 4th segment—a condition probably reached about the 6th or 7th stage, but I have not paid sufficient attention to the circulation to be more precise.

Stages 11, 12, *&c.*

If the nymph is not going to hatch out at the end of the 10th stage, the antennæ do not change from the 6-segmented condition. It seems to be a rule in *Agrion* and *Ischnura* that the 7-segmented condition only exists in the final stage, while in *Pyrrhosoma* the only two individuals which I reared through the last stages showed the 7-segmented condition in the penultimate stage.

The labium may have either 6 or 7 hairs on each palp and 5 or 6 pairs on the body, while occasionally no further development takes place after the 10th moult. If there are 7 hairs on each palp they are very crowded and the 7th appears at the extreme base of the palp.

The majority of my nymphs hatched out into imagines at the end of the 10th, 11th, or 12th moults. Two Agrions passed through 13 stages, while the two Pyrrhosomas passed through 11 and 12 respectively. A single *Enallagma* passed through 14 stages as did *Erythromma*, while an *Ischnura* imago emerged at the 12th moult. I shall later on discuss the question of the variation in the number of moults in nymphs of the same species.

THE MOULTS.

In the case of the Agrion nymphs which hatched from the eggs at the end of August, the first moult took place in from 8 to 12 days. Their average length, after hatching, was 1·3 mm., while after the first moult it was 1·6 mm. The second moult was a less regular event than the first, some nymphs undergoing it 14 days later, while others took more than three weeks to complete their second stage. The third moult again took place from a fortnight to five weeks after the second, while the fourth was even more irregular than the third.

At the beginning of November the nymphs become very sluggish, showing but little interest in the *Paramœcia* with which they were abundantly supplied.

In the beginning of December, seeing that matters were at a standstill, I placed 18 of the tumblers in a Hearson incubator and maintained a fairly constant temperature of 19° C. (66·2° F.), which is a very high summer temperature. The outer door of the incubator was removed, so as to admit light, but, from the position in which the incubator stood, the occupants had little more than twilight even on the brightest days.

The effect of the warmth was soon obvious, as all the nymphs in the incubator showed great activity and readiness to feed. One nymph moulted 8 days after being placed in the incubator, and others followed fairly soon. By the end of February several of the nymphs had completed their 8th stage, while one was through its 9th and another through its 10th. During the same time the nymphs, some fifty and more, in the ordinary temperature of the laboratory did not moult at all, with the exception of three specimens, two of which moulted at the beginning of December and the other at the end of February. The average length of the nymphs in the incubator was 11·0 mm., while that of those outside was 2·7 mm. !

A large part of the experiment had now to be sacrificed, as I was leaving Norfolk for Ireland, so the incubator was gradually cooled off and the former occupants became less active and much less hungry. On April 20th I started a similar incubator in Larne, and this was kept going until July 10th, but only one or two of the nymphs which had been kept warm during the winter were placed in it, a number of the less advanced ones being selected in order to further test the effects of temperature. The new batch of nymphs quickly showed great activity and keen appetites and began to grow rapidly, moulting at short intervals. If further evidence were needed of the effect of temperature in the causing of moults, it is to be found in the cases of three nymphs, one in the 5th and two in the 6th stage, which had stagnated for 92, 135, and 104 days respectively through the winter. They were placed in the incubator for 21 days in February. Each moulted 7 days after being warmed, and each moulted a second time in the next 10 days. After being removed from the incubator one moulted three weeks later, while the other two were five weeks without changing.

This effect of temperature upon the duration of the stages makes it impossible to find a fair average duration for any stage except by using only those nymphs which have been incubated, and only those stages passed through while in the incubator. Unfortunately, this was not foreseen, so that the material at hand is very meagre. I have, however, prepared a table showing for 19 nymphs the number of days occupied by each stage, indicating the days passed in the incubator by using a thicker type (*v.* Table 1).

From Table 1, reading down the columns and only using the figures for stages begun and completed in the incubator, we can

TABLE 1.—Showing the number of days occupied by each stage of the nymph. The figures in thick type indicate that those days were spent in the incubator.

STAGE …………	Nymph.	Sex.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.	XIV.	Total number of days.
A. pulchellum.	†1.	♂ …	12	17	14	25	150	16 + **15**	**22**	**5**	**21**	**18** + 12	86 *		211	…	624
”	‡2.	♀ …	8	14	18	60 * + **19**		**20**	**8**	**14**	**20** + 74	41	…	…	…	…	296
”	‡3.	♂ …	12	20	21	46 + **10**	**9**	**10**	**11**	**16**	**25** + 28	69	…	…	…	…	277
”	‡4.	♂ …	12	17	14	57 + **12**	**9**	**12**	**10**	**14**	**14**	**10** + 48	…	…	…	…	229
”	†5.	♀ …	12	21	32	166 + **2**	**9**	**31**	**14**	**23**	**2** + 35	234	50	…	…	…	634
”	†6.	? ..	7	17	14	25	92 + **7**	**9**	**6** + 21	31 + **15**	**17**	**24**	**25** + 29	…	…	…	339
”	‡7.	? ..	11	24	55	2 + **15**	**4**	**10**	**7**	**8**	**9**	**22**	**6** + 81	37	…	…	291
”	†8.	♀ …	…	…	? + **15**	**13**	**9**	**14**	**12**	**14**	**4** + 8	27	26	37	217		
”	†9.	♀ ..	…	…	…	? + **11**	**17**	**14**	**21**	**18**	40	49	227				
”	§†10.	♂ …	…	…	…	11	28	135 + **7**	**6**	**3** + 38	16 + **11**	**36**					
”	§†11.	♂ …	…	…	14	23	26	104 + **7**	**8**	**1** + 37	16 + **7**	**22**	**52** + 12				
”	†12.	♂ …	…	…	13	7	35	133	38	16 + **18**	**14**	**49** + 8					
”	‡13.	♂ …	…	…	…	14	28	60 + **10**	**9**	**10**	**14**	**17**	**21** + 37	69			
”	‡14.	♀ …	…	…	…	13	14	28	51	2 + **10**	**17**	**24**	**30** + 37	71			
I. elegans.	‡15.	? …	…	…	14	21	34	26 + **8**	**7**	**12**	**15**	**9**	**22**	**8** + ?			
Er. naias.	‡16.	? ..	…	…	…	…	28	60 + **19**	**20**	**13**	**8**	**13**	**8** + 2	51	37	56	
En. cyathigerum.	†17.	? …	…	…	…	…	7	23	193	6 + **11**	**12**	**12**	**44**	**2** + 63	216	30	
P. nymphula.	‡18.	? …	…	…	…	19	23	32	28 + **14**	**13**	**13**	**13**	**21**	**7** + 74			
”	‡19.	? …	…	…	…	13	39	53 + **14**	**13**	**13**	**16**	**25** + 18	83				

* A moult was by mistake not recorded; in No. 2 it occurred in the incubator.

† Only in incubator from April 20th onwards; not during the winter.

‡ Only in incubator during the winter months—December to February.

§ Incubated for 21 days in February, otherwise no winter warmth.

find the average number of days occupied by each stage, and the results, so far as it is possible to get any, are as follows:—

Table 2.

Stage.	Average number of days.	Number of nymphs.	Max. number of days.	Min. number of days.
V.	9·5	6	17	4
VI.	15	8	31	9
VII.	12·0	14	22	6
VIII.	13·3	13	23	5
IX.	14·1	12	21	8
X.	19·2	10	47+	9
XI.	29·4+	5	52+	10

The figures indicate that the stages tend to lengthen from the earlier to the later ones. There is, however, a source of error in the method used, and that is that while some nymphs are full-grown at the end of the tenth stage, others go through 11, 12, 13, or 14 stages. Now one point which is quite clear without any statistics is that the final stage is always a fairly long one, and this fact will of course affect the above figures. I have therefore checked these results by using Table 1 in another way. I have taken the average duration of the last stage of each nymph, then of the penultimate stage, then of the one before that, and so on as far back as my figures will permit, again of course only including stages begun and completed in the incubator, and the results are as follows:—

Table 3.

Successive stages	4—8	5—9	6—10	7—11	8—12	Penultimate Stage. 9—13	Last Stage. 10—14
Number of nymphs	4	11	14	15	11	6	3
Average no. of days	12·3	10·7	13·4	14·7	16·8	19·5	45·6+
Max. & min. no. of days	17. 10.	22. 8.	31. 5.	44. 6.	24. 9.	24. 14.	52+ 36.

Again the figures show that the stages tend to lengthen out as the nymph grows bigger.

The first imago to appear emerged 33 weeks (230 days) after hatching from the egg and after passing through 10 stages. This was one of the individuals which spent the winter in the incubator, and I expected to find that all the nymphs which had been kept warm during winter and had fed and moulted regularly would complete their life in the same number of stages. However, out of ten such nymphs only three got through in 10 stages, one in 11, five in 12, and one in 14. The three nymphs which completed in 10 stages were placed in the incubator in their 4th stage, as was also one which passed through 12 stages, while all the other nymphs were in their 6th, 7th, or 8th stages at the beginning of December. Now all these nymphs were in the incubator at the same time and for 81 days, and during that time they moulted a number of times, varying from 3 to 7. If we consider the number of times that each of those nymphs moulted in relation to the total number of moults it passed through, we find that those introduced into the incubator in stage 4 passed through half (5 out of 10 and 7 out of 12) their total number of moults in the 81 days, while those introduced at later stages passed through less than half their total number—a fact which supports what I have already shown by two other methods, namely, that the stages tend to lengthen out as the nymphs advance.

Whether or not this lengthening out of successive stages is a phenomenon common to the larvæ of all insects has still to be shown, and I can find no reference to the subject, but it is interesting to note that Newport (1839) mentions that the rate of the pulse in the larvæ of *Sphinx ligustri* gets slower in successive stages—a fact which might well be correlated with the lengthening of the stages.

Leaving out for the present the question as to whether the winter warmth has curtailed the number of the stages, a point on which I have very little evidence, it is easy to show that the favourable conditions greatly curtailed the duration of the life of the nymph.

All the imagines from the winter-warmed nymphs appeared between April and July of the year following that in which the eggs were laid—that is, within 10 months. On the other hand, the imagines from the nymphs which were in ordinary laboratory temperatures during the winter, with one exception, appeared a year later than the others, more than 20 months after the hatching of the eggs, and in spite of the incubation from April to July. In connection with these two extremes, the three cases of nymphs which for 21 days in February enjoyed the warmth of the incubator are most interesting. In all other respects they were treated exactly like the second batch of nymphs—that is, they endured ordinary laboratory temperatures until April 20th, and then were in summer temperature,—yet they all three hatched out with the first batch, one in June, one in July, and the third in August. It is certainly interesting that three weeks' warmth in February, during which each nymph moulted twice, should have made a difference of more than 10 months to those three nymphs; and since temperature has such a marked effect it may be possible to account for the periodic swarms of dragonflies on the ground that a specially mild winter in some region may bring on a batch of nymphs, so that the imagines appear a season earlier than under normal circumstances. In such a case the batches of 2 years would appear together, and might be a prelude to a migration.

I cannot account for the single individual which, without any winter warmth, emerged with the first batch of nymphs. It is possible that it was in the incubator with the other three in

Table 4.

No.	Nymphs in incubator from Dec. 7, 1906, to Feb. 26, 1907.		Nymphs in incubator for 21 days in Feb. and again from April 20, 1907.		Nymphs left cold through winter. Incubated from April 20, 1907.	
	Imagines hatched out.	No. of Stages.	Imagines hatched out.	No. of Stages.	Imagines hatched out.	No. of Stages.
1 ...	*A. pulchellum*, Apr. 15, 1907.	X.	*A. pulchellum*, June 5, 1907.	X.	*A. pulchellum*, June 5, 1907.	X.
2 ...	,, June 2, ,,	X.	,, July 22, ,,	XI.	,, May 24, ,,	XIII.
3 ...	,, ,, 12, ,,	XII.	,, Aug. 8, ,,	XI.	,, ,, 10, ,,	XIII.
4 ...	,, ,, 14, ,,	XII.			,, ,, 21, ,,	XI.
5 ...	,, ,, 21, ,,	X.			,, ,, 24, ,,	XI.
6 ...	,, ,, 24, ,,	XII.			*E. cyathigerum*, May 14, ,,	XIV.
7 ...	*I. elegans*, Apr. or May, ,,	XII.				
8 ...	*P. nymphula*, May 11, ,,	XII.				
9 ...	,, June 6, ,,	XI.				
10 ...	*E. naias*, July 22, ,,	XIV.				

February, as it moulted once during that period, but so far as my records go it was not!

Table 4 (p. 272) gives the dates of appearance of the imagines and also the number of stages through which the nymphs passed.

With regard to the question whether a high temperature in winter tends to reduce the number of stages in the life of the nymph, the material is too scanty to form any sound opinion. For such a question only one species can be considered at a time, as probably all species do not moult the same number of times under similar conditions. Also the individuals of any one species will not, under apparently similar conditions, all moult the same number of times, so that the average of a fair number of individuals would be necessary to get any definite result.

With regard to *Agrion pulchellum*, the only thing that can be said is that, with the single exception already referred to, the only nymphs which completed in 10 stages were three which had been incubated during the winter, while the only ones which passed through the 13 stages were two which had been kept cold during the winter. On the other hand, three of the winter-warmed nymphs passed through 12 stages, while two of the others got through in 11; and I am inclined to think, after studying the rate of growth, that the incubator did nothing towards reducing the number of stages. I shall discuss this in relation to the question of body-length.

Body-length.

The average length of a nymph of *Agrion pulchellum* in its final stage is 18·0 mm., the smallest nymphs being about 14·0 mm. and the largest about 22·0 mm. These figures were obtained by measuring a number of nymphs with 7-segmented antennæ collected without any regard as to the number of stages they had passed through, and they show a wide range of variation in size. In the newly-hatched nymphs there was but little difference in body-length, but at each succeeding moult the differences became more marked, so that, for instance, after the eighth moult, two nymphs measured respectively 6·7 mm. and 14·0 mm. In noting this fact I also noted that the smaller nymph passed through 13 stages, while the larger one completed in 10; and as the latter had been incubated during the winter, while the former had not, I at first thought that there would be evidence of reduction in the number of moults in the winter-incubated individuals. To test this I took the body-lengths of all the nymphs, so far as I had the figures, at each stage, and compared the length of each nymph in relation to the number of moults it ultimately went through, and the results are rather interesting and are given in Table 5 (p. 274). It will be noticed that the tendency all through is for the larger nymphs in any stage to be those which ultimately complete in the smallest number of stages; and since this is noticeable in the beginning of the second stage and becomes more marked in succeeding stages, it seems that the earlier stages

TABLE 5.—Showing the body-lengths of different nymphs at the commencement of the stages, and also showing the total number of stages through which each nymph ultimately passed. It will be seen that the tendency is for the larger nymphs of any stage to ultimately get through in the smallest number of stages.

No.	Beginning of Stage I.		Beginning of Stage II.		Beginning of Stage III.		Beginning of Stage IV.		Beginning of Stage V.		Beginning of Stage VI.		Beginning of Stage VII.		Beginning of Stage VIII.		Beginning of Stage IX.		Beginning of Stage X.	
	Body-length.	Total No. of Stages.	Body-length.	Total No. of Stages.	Body-length.	Total No. of Stages.	Body-length.	Total No. of Stages.	Body-length.	Total No. of Stages.	Body-length.	Total No. of Moults.	Body-length.	Total No. of Moults.	Body-length.	Total No. of Moults.	Body-length.	Total No. of Moults.	Body-length.	Total No. of Moults.
1...	1·43	XI.	1·83	X.	2·44	X.	3·08	X.	5·03	X.	6·45	X.	9·60	X.	10·33	X.	14·0	X.	17·02	X.
2..	1·41	X.	1·71	XI.	2·32	X.	3·00	X.	4·10	X.	5·46	X.	7·05	X.	10·14	X.	10·93	X.	13·75	X.
3..	1·38	XII.	1·65	X.	2·19	X.	2·92	X.	4·02	X.	5·31	XI.	6·48	XI.	9·60	X.	9·45	XI.	10·58	XI.
4..	1·32	X.	1·63	X.	2·18	XI.	2·87	X.	3·91	XII.	5·22	X.	6·35	XI.	8·44	X.	9·19	XI.	10·19	XII.
5..	1·32	X.	1·62	XI.	2·17	XI.	2·80	XII.	3·81	X.	5·00	X.	5·46	XII.	8·03	XI.	8·00	XI.	10·11	XII.
6...	1·30	XI.	1·52	XIII.	2·11	XI.	2·80	XI.	3·68	XII.	4·43	X.	5·44	X.	7·50	XI.	7·96	XII.	10·02	XI.
7...	1·23	XIII.	1·51	XII.	2·09	X.	2·80	XI.	3·58	XI.	4·31	XII.	5·38	XI.	7·46	XII.	7·70	XII.	9·89	XII.
8...	...	...	...	...	2·02	XIII.	2·75	XII.	3·47	XII.	4·30	XII.	5·34	XI.	7·04	XI.	7·27	XIII.	8·75	XIII
9...	...	...	...	...	1·82	XII.	2·63	XIII.	3·00	XI.	4·25	XI.	5·11	XII.	6·46	XIII.	6·72	XIII.	7·85	XIII.
10...	...	...	...	...	...	...	2·61	XIII.	2·93	XIII.	4·09	XI.	4·84	XIII.	6·21	XIII.				
11...	...	...	...	...	...	...	2·57	XI.	...	...	4·02	XIII.	4·50	XIII.	6·14	XII.				
12...	...	...	...	...	...	...	2·45	X.	...	...	3·99	XII.								
13...	...	...	...	...	...	...	2·40	XII.												

of the nymph decide its destiny as to the number of stages. Incubation, then, had apparently no effect on the number of stages which had been determined before incubation was resorted to, but it seems probable that if the nymphs had been incubated from the moment they hatched, the effect would have been different. That there is not complete regularity in the Table is perhaps not to be wondered at. A nymph may "stagnate" for a period owing to some upset of its metabolism, and that might cause it to fall behind for a stage or even longer, in which case the question arises whether a long delay would not possibly necessitate an extra moult? I will consider this point further when discussing the significance of the moult.

The Antennæ.

The segmentation of the antennæ has already been described. It is to be noted that the segment immediately above the scape, *i. e.* the third from the base, is the one which divides three times to produce new segments for the antenna, and that these divisions are, with a very few exceptions, definitely connected with certain stages in the life of the nymph. The actual formation of the new segment is not, of course, an instantaneous process, but takes place by slow degrees within the "shell" of the antenna, only becoming revealed when that shell is cast off.

It is interesting to note that in one of the Ephemeridæ, where development has been followed, Lord Avebury (1863 and 1865) found that the third segment of the antenna, the one next to the scape, is there also the centre of growth.

As the nymph increases in length the antennæ also grow, but these organs do not maintain a rate of growth proportionate to that of the body. Whereas in the first stage the antennæ are 23 per cent. of the body-length, the percentage gets steadily less as the nymph grows, until, in the full-grown individual, the antennæ are less than 12 per cent. of the body-length.

The growth in length of the antenna is not due to the gradual lengthening of each segment, but is chiefly due to growth of the region immediately above the scape. This is easily shown by taking the average length of the antenna at each successive stage and finding what percentage of that length is taken up by each segment. The results are shown in the accompanying chart (p. 276), from which it will be seen that, whereas segment 3 gradually increases its percentage of the length of the antenna, the scape and segments 4 and 5 only maintain a rate of growth proportional to that of the antenna, while segment 6 grows much too slowly to maintain its proportion to the total length.

Stages X., XI., XII., and XIII. may any of them be the last stage in the life of the nymph, and in finding the average length for each segment at each stage I had to exclude the "7-segmented" individuals in each of these stages, except XIII., where there were no "6-segmented" nymphs. For comparison I also found the percentage for the "7-segmented" condition in stages X., XI., and XII., and they are given as X. *a*, XI. *a*, and XII. *a*, and it will be seen that in each of them segment 3 is proportionately longer than in the "6-segmented" condition. The average length of the "7-segmented" antennæ is also greater than that of the "6-segmented" antennæ for the same stage, indicating that the larger nymphs of the stage are those which are near their final ecdysis.

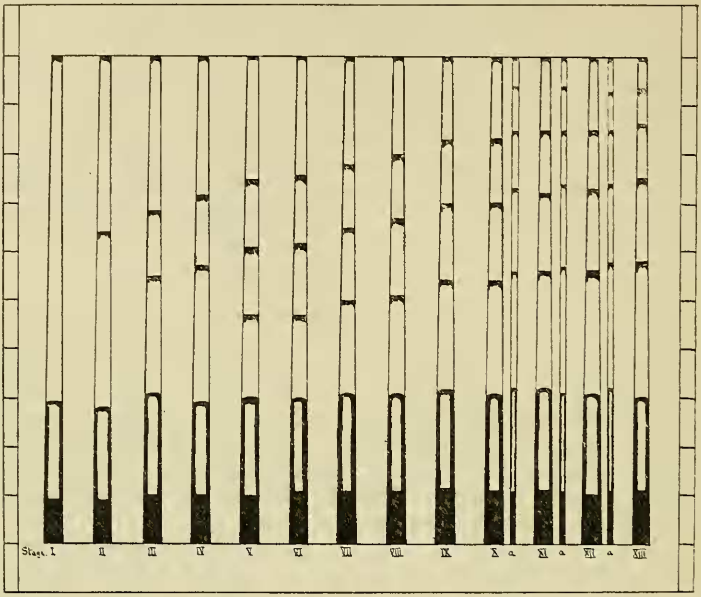

Chart showing the growth of the segments of the antennæ in *Agrion pulchellum* Lind.

The Lamellæ.

Like the antennæ, the lamellæ are much longer in proportion to the body-length in the newly-hatched nymph than in the full-grown one. Whereas they are almost the same length as a nymph of 1·3 mm., in a nymph of 17 mm. they are less than half the length.

The pointed linear organs of the first-stage nymph gradually widen out in the vertical plane and ultimately become leaf-like. In both *Agrion pulchellum* and *puella*, and perhaps in all species of this genus, they gradually lose their pointed appearance and become distinctly rounded at the apex. Not only have I observed this rounded character in nymphs reared from the egg, but I have repeatedly hatched out the imagines of both these species, and only those nymphs with rounded lamellæ produced Agrions. I mention this because Lucas (1900, pp. 281, 288) describes the lamellæ of *A. puella* as being always pointed, and says that those of *A. pulchellum* are apparently similar. He mentions, however, that some authors have described them as having rounded apices. The full-grown nymph with pointed lamellæ, which is otherwise almost (or quite ?) indistinguishable from the Agrions, is *Ischnura elegans*.

The lamellæ of *Agrion*—I have been unable to find a character to distinguish the nymphs of *A. pulchellum* and *puella* from one another—are indistinguishable at first from those of *Ischnura*, unless possibly by certain small patches of pigment; but about the 6th, 7th, or 8th stage, sooner or later, according to the size of the nymph, they have become sufficiently wide and rounded at the apex to distinguish them.

These organs, into which the lateral tracheal trunks of the body pass and in which they break up into minute branches, so that the whole lamella is filled with them, are said to have a respiratory function. I have already referred to the intermittent blood-stream in these organs. Whether it is correct to describe it as intermittent I am not sure, but I have several times noticed that in a nymph taken from the tumbler and placed under the microscope no circulation was to be detected until after the lapse of some time, and it has occurred to me that the circulation in the lamellæ was noticeable only when the air in the water was becoming exhausted.

These organs are not, however, indispensable, as the nymph can live quite well without them. In the final stage they are often without them, having apparently cast them off. In the earlier stages, however, if a lamella is removed it is replaced by degrees. If two or three days previous to a moult a lamella is removed, no replacement takes place until the second succeeding moult. As soon as the nymph escapes from the old skin, a very thin pointed sac, more or less circular in transverse section, is visible in place of the lamella previously removed. This sac is much smaller than the other lamellæ and contains at first no trace of tracheæ. It takes two, three, or even four moults before a new lamella is indistinguishable from the uninjured ones. The process of renewal is not sudden as it appears to be. The wound caused by removing a lamella is apparently quickly closed and the formation of the new lamella commences within the "shell," I believe at the time when a new nymph-skin is forming within the old one. Presumably it forms in a crumpled condition like the imaginal wings within the nymph wing-cases, and as soon as the pressure of the outer shell is released, the new lamella expands as a sac, becoming turgid owing to fluid entering it from the body.

A leg is replaced in the same way as a lamella, taking two or three stages to attain perfection, appearing immediately after the moult as a thin-walled sac which gradually thickens and hardens.

I have paid very little attention to the replacement of lost parts, but it seems to involve two processes: first, the formation of a thin-walled sac in the form of or tending towards the form of the organ to be renewed, and, secondly, a re-formation within the sac of the muscular and tracheal systems.

WING DEVELOPMENT.

I have already mentioned that the first sign of the pleural ridges appears after the nymph has completed its third or fourth moult. This statement is true of *Agrion*, *Ischnura*, and *Pyrrhosoma*, and may be true of *Enallagma* and *Erythromma*, but I imagine that in these cases wing-development begins rather later. These ridges lie diagonally across the second and third thoracic segments on either side of the tergum, and are the result of the upward growth of the pleura of the meso- and metathorax.

The rate of development from the first differs somewhat in different individuals. In the stage succeeding that in which the ridges first appear there may be a small bud on the inner side of each ridge, representing the commencement of the "wing," or this may not appear until a stage later.

As the buds grow larger the ridges also develop, those of the mesothorax gradually spreading anteriorly over the tergum until they meet in the middle line. Posteriorly they do not approach one another, so that a triangular patch of the tergum is left exposed between them. The metathoracic ridges join on to the posterior edges of the mesothoracic ones, and taper away posteriorly towards the sides of their segment, the posterior margin of which they slightly overlap. Thus a large part of the tergite of the metathorax is left exposed. The "wings" develop in such a way that they lie more or less flat on the sides of the dorsum in the wedge-shaped depression between the ridges, and extend backwards over the anterior abdominal segments. Towards the end of the final stage, however, when the thorax of the imago is forming within that of the nymph, the "wings" are somewhat raised and tilted.

At each moult an advance in development is visible, but it differs very considerably in the earlier stages in different individuals. For instance, a condition when the anterior "wings" just overlap the posterior edge of the metathorax, and the posterior wings just cover the first abdominal segment, might represent the 8th, 9th, or 10th stages, apparently depending on the general body-growth of the nymph and the number of stages through which the nymph is going to pass. There is a distinct connection between the later moults and the proportion of increase in the length of the wings. For instance, if the anterior wings reach in one stage almost to the posterior margin of the metathorax, their increase at the next moult will be about 33 per cent. of their length. At the next moult the increase will be about 40 per cent., while at the next, whether the 10th, 11th, or 12th, &c., the increase will be about 50 per cent. This is a large increase, and is, in every case I have observed, evidence that the nymph has reached its final stage. The "wings" now cover the first three abdominal segments, and often extend halfway over the fourth, and any nymph found with such long wing-cases is in its last and generally its longest stage.

The last nymphal stage is characterized by these long "wings" and by the 7-segmented antennæ, and the one or two stages previous to that are fairly well-marked by the rapid growth of the wings. The first four stages in the life-history are also easily recognized by the state of the antennæ and of the mask. In my experience it was, with only one or two exceptions, after the antennæ had become six-segmented that the nymphs showed such variation in their rate of progress even when under similar conditions.

Respiration.

The caudal lamellæ have been described as respiratory organs, and have been called "caudal gills," but Dewitz (1890) pointed out that the nymph can live without them, and suggested that possibly a rectal respiration, similar to that of the Calopterigidæ and the Anisopterids, existed in the Agrionidæ also. In those forms, however, where rectal respiration is dominant, there is an elaborate arrangement of tracheæ in the walls of the rectum which is completely absent in the Agrionidæ.

Dewitz has shown that a stream of water does pass in and out of the rectum in the Agrionidæ, but from my observation it is a very weak one, nor is there any special apparatus surrounding the anus in this group to prevent ingress of foreign particles such as is found in the Anisopterids. If rectal respiration exists at all, it seems to me that it must be very slight and of but little importance, as I could not observe any increased number of contractions of the rectum in specimens of *Agrion* which had been deprived of their lamellæ.

In the absence of the lamellæ, I think the whole of the respiration must be carried on through the skin.

Conclusion.

The occurrence of a pronymph stage in the Odonata * is not unique. It has been observed by Pagenstecher (1864, p. 7) in *Mantis religiosa*, and occurs also in other Orthoptera [see Künckel (1890 (1) p. xxxvii, and 1890 (2) p. 657)], and in several other orders (Packard, 1898, pp. 583–585), and is no doubt more common than has at present been recorded.

The stage is apparently for the purpose of freeing a tightly-packed larva from the egg, the amnion, instead of breaking and remaining within the shell, continuing intact until after the larva is clear, and the amnion forms the pronymph skin.

In the Odonata the larva casts the pronymph skin in exactly the same way as it casts its skin in subsequent moults, and it appears that, in the other forms in which this stage has been observed, the amnion is got rid of in much the same way, except that, as a rule, a special ampulla exists in the thorax of the larva which, by swelling up, bursts the amnion in that region (Packard, *l. c.* p. 584).

Although the total number of moults may vary somewhat, there is an unmistakable connection between certain stages in the development of the nymph and certain moults. What I have said as to the growth of the antennæ, the appearance of the labial hairs, and the development of the wings shows this, especially in the earlier stages, and it is possible that a large number of nymphs kept under uniform conditions might have caused the correspondence to have continued through every stage.

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* Exactly the same phenomenon occurs in *Sympetrum striolatum*, one of the Anisopterid dragonflies, where the pronymph stage continues for about 7 minutes.

The correspondence between certain stages in development and certain moults has been observed in the larvæ of other insects. For instance, Acrydians moult five times, the wings appearing after the second moult and increasing quite definitely at each succeeding moult, the increase in the last stage being very great. "Besides the acquisition of wings there are slight differences at each moult both in structure and colour, besides size, so that we may always recognise the comparative age and the particular stage of growth of any individual" (Packard, *l. c.* p. 595). Lord Avebury (*l. c.* p. 62) noticed that the nymph of *Chloëon* "gradually attains its perfect condition through a series of more than 20 moultings, each accompanied by a slight change of form," and there are numerous other cases cited in works on entomology, but, by many authors, no notice seems to have been taken of these facts in discussing the question of the significance of the moult.

On this latter point various suggestions have been made, of which the simplest, and perhaps the oldest, is that the moults are necessary to enable the larva to grow. It is obvious that where a larva is encased in a hard integument, one of two processes is necessary in order that the contained organism may increase in size. Either the integument must be capable of expanding with the organism, or it must be cast off from time to time.

When the nymph moults it expands greatly in size as it creeps out of its old skin, and, a few minutes after escaping, is much larger than the skin from which it emerged. The nymph has therefore been in a state of compression within its skin previous to the moult. But growth does not only take place at the moment of the moult—for instance, a nymph measuring 11 mm. at the commencement of its final stage was 15·2 mm. at the end of it, so that the nymph-skin is undoubtedly capable of expansion.

On the other hand, Dr. Sharp (1895, p. 163) considers that growth is only of secondary importance in accounting for the moult, urging as one reason that "many insects make their first ecdysis almost immediately after they leave the egg"; and he quotes the case of the blowfly larva, which, "according to Lowne, moults within two hours of its emergence from the egg." The case of the dragonfly pronymph is even more apt in this connection.

Eisig (1887, p. 781) suggested that the moult was for the purpose of getting rid of waste nitrogenous matter, and Dr. Sharp (*l. c.* p. 163) adds that it may be of importance in separating the carbonaceous products from the blood. Bataillon (1892, p. 61; 1893, p. 18) has stated that at the period of the moult the larva is in a state of asphyxiation; and Dr. Sharp (*l. c.* p. 131), referring to this observation, remarked that if it is a fact, "the secretion of the new coat of chitin may figure as an act of excretion of considerable importance."

The method of passing to the integument certain waste products of the metabolism is almost universal throughout the animal kingdom, and there seems no reason why it should be regarded as, in insects, a special process of excretion. Whatever may have been the primary cause, the process has apparently been seized upon by Natural Selection, which has eliminated the less protected individuals, and produced a tough protective exoskeleton.

Bataillon's observations do not seem to me as important as Dr. Sharp regards them in demonstrating that the moult is a special act of excretion. When it is remembered that the larva, immediately after a moult, is soft and helpless, unable to feed, and an easy prey to almost any hungry animal, it is possible to believe that those individuals which did not quickly produce a new protective armour were eliminated in the struggle for existence. In order to quickly produce a new hard skin, a larva would necessarily retain a large amount of waste products which would otherwise pass out of the system, and this might account for an asphyxiated condition immediately prior to the moult.

Pantel (1898) considered the moult as necessary to account for the formation of ectodermal organs, and points out that, at each of the three stages of the larva of *Thrixion*, new characters appear; while Packard apparently held much the same view, as he says (*l. c.* p. 615), "the swollen bodies of the gravid female of *Gastrophysa*, *Meloë*, or of *Termites* and of the honey-ant show that the skin can stretch to a great extent, but in the metamorphoses of Crustacea and of Insects, the young of which are more or less worm-like or generalised in form, with fewer segments and appendages, or with appendages adapted for quite different uses from those of mature life, the necessity for a change of skin is seen to be necessary for mechanical reasons. Hence Crustacea and Insects moult most frequently early in life, when the changes of form are most thoroughgoing and radical, while simple growth and increase in size are most rapid at the end of the larval life, as seen in both shrimps and crabs, and in insects."

Now it seems to me that the fact that the larva is in a state of compression within the old shell at the time of the moult, suggests that the moult is necessary for growth, while the fact that certain stages of development are correlated with certain moults suggests that the moult is necessary for development, and I am inclined to think that a moult may be either a "growth-moult" or a "developmental moult," or a combination of the two.

Growth and development are, to some extent at least, independent phenomena, since we find variations in size in equally mature individuals, and apparently either growth or development may be retarded without the other being affected, at any rate to the same extent.

From the fact that certain stages in the life-history of a larva are correlated with certain advances in development, growth cannot possibly control the moults producing those stages, and they must be primarily "developmental moults." Further, assuming that there are ectodermal developments to take place, it seems to me that so long as those developments do not take place in stages of excessive length, development will always be the controlling factor.

From the time of the moult the new ectoderm of the nymph is steadily hardening (probably oxidizing), and gradually losing its elasticity. As soon as the skin has ceased to expand with the growth of the nymph, the pressure on the body of the nymph reacts so that a new layer of chitin is laid down within, and separate from, the old layer. Once this new layer has completely isolated the old one the latter becomes brittle, and gives way along a line of weakness in the median line of the thorax when the nymph exerts itself and escapes. Such would be the explanation of a "growth-moult" pure and simple. If, however, previous to this condition being reached a developmental stage had been arrived at, a moult will take place which will serve both purposes, but will have been caused by developmental requirements.

In the case of one of my nymphs two moults took place within 4 days of each other. The second moult could not have been required for growth nor, on the excretion theory, for excretory purposes, and I imagine that the first moult was a "growth-moult" and the second a "developmental" one, especially as the first moult was the first to take place after the nymph had been put into the incubator, and 17 days after the previous one.

In this connection the effects of temperature on the number of moults are important. Packard (*l. c.* p. 616) refers to the experiments of Weniger and others on the larvæ of certain Lepidoptera, the results of which show that under warm moist conditions the number of moults is reduced from 5 to 4; and referring to certain other experiments, he says (p. 618): "As to the cause of the great number of moults in the arctians and in the beetles experimented with by Riley, it would seem that cold and lack of food during hibernation were the agents in arctians, and starvation or the lack of food in the case of the beetles, such cause preventing growth, though the hypodermis-cells retained their activity." W. H. Edwards states that larvæ of Lepidoptera which hibernate moult more often than those which have only a summer existence, and larvæ with a wide geographical distribution moult more often in cold than in warm regions. He also says "there seems to be a necessity with hibernators of getting rid of the rigid skin in which the larva has passed the winter; that is, if hibernation has taken place during the middle stages, as it does in *Apatura* and *Limenitis*. In these cases, very little food is taken between the moult which precedes hibernation and the one which follows it, and the larva, while in lethargy, is actually smaller than before the next previous moult. The skin shrinks, and has to be cast off before the awakened larva can grow" (quoted from Packard, *l. c.* p. 615).

Such a moult as that described by Edwards is apparently a "growth-moult" pure and simple. Unfortunately, however, it is not always so easy to determine the nature of a moult Development involves a certain amount of local growth which presumably proceeds steadily between the moults. If a "growth-moult" is interpolated, the ectodermal structures will not remain as they were before the "growth-moult," but will show some advance as the result of that moult, so that, if in the ideal individual there are a definite number of developmental stages each showing a definite advance, the interpolated "growth-moult" upsets this state of things. But the developmental stages must get right again by the end of the larval period, so that there must be some power of adjustment; in other words, the interpolation of a single "growth-moult" will not necessarily add merely one moult to the life-history, but may necessitate one or more additional developmental moults for adjustment. The more normal moults in the life-history, the more probable it will be that the developmental stages will be complicated by stages for adjustment. The lengthening of the later stages of larval life, which Packard (*l. c.* p. 615) regards as chiefly growth-stages, seems to me to be a lengthening of the developmental stages owing to the more radical changes which they involve. The last stage of the nymph, for instance, in which the most marked internal changes take place is always a long one and corresponds with the pupal stage of the Holometabola.

The fact that certain moults have nothing whatever to do with growth (*e. g.*, of the pronymph of the dragonfly; of the sub-imago of Ephemerida; moult to pupa and imago, &c.) seems fatal to a theory that growth is the cause of the moult, while the fact that certain moults have apparently nothing to do with development (*e. g.*, the moult of larvæ after hibernation) seems fatal to a theory which makes development the cause of the moult. Since, however, both causes seem to be at work, it is possible that both theories, combined and readjusted, may give us a true explanation of the significance of the moult.

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EXPLANATION OF THE PLATES.

Plate XXXIII.

Development of Agrionid Dragonflies.

Fig. 1. The egg of *Ischnura elegans* Lind., some hours before hatching.
Fig. 2. Part of the same egg, at a later stage, showing the shell-rupture and the vesicle formed, and the head just commencing to move forward.
Fig. 3. Part of the egg, at a still later stage, showing the head × almost filling the vesicle. *a* is the point at which the membrane will rupture for the escape of the pronymph.
Fig. 4. The pronymph immediately after its escape from the egg.
Fig. 5. Prothorax, dorsal view, of the imago of *Agrion puella* L., ♀.
Fig. 6. Prothorax, dorsal view, of the imago of *Agrion pulchellum* Lind., ♀.

Plate XXXIV.

Development of Agrionid Dragonflies.

Figs. 1, 2, 3 show the last stages of wing-development in the nymph of *Ischnura elegans* Lind., in this case stages 10, 11, and 12. The drawings are from the moulted skin.
Fig. 4. The "mask" of *Agrion pulchellum* Lind., in the first stage, upper side.
Fig. 5. One of the labial palpi of the same "mask" × about 400.
Fig. 6. The "mask" in the third stage.
Fig. 7. The "mask" in the seventh stage, showing the palpi almost closed down on the anterior border of the labium. The stiff hairs are so situated that when the nymph is feeding they assist in holding the food, the mouth being situated just above *b*.

4. Growth-Stages in the British Species of the Coral Genus *Parasmilia*. By W. D. Lang, M.A., F.Z.S., British Museum (Nat. Hist.).

[Received February 16, 1909.]

(Text-figs. 38–46.)

I. Carruthers' "Phases" in Carboniferous Corals.

In the early numbers of last year's 'Geological Magazine' an article by R. G. Carruthers appeared on some simple Carboniferous Corals *. In it stress is laid on the necessity of cutting serial sections of corals and for the determination of species according to their growth-stages. It is shown that Carboniferous corals previously described as various species of *Zaphrentis* are really different forms of *Caninia cornucopiæ* Michelin, and that during development five "phases" can be recognised, occurring in the following order: (1) that corresponding with *Zaphrentis vermicularis* de Koninck; (2) with *Lophophyllum dumonti* Edwards & Haime; (3) with *Zaphrentis nystiania* de Koninck; (4) with *Zaphrentis edwardsiana* de Koninck; (5) with *Caninia cornu-bovis* Michelin.

It is important that the term "phase" is used to designate these forms and not the implicatory "stage," and the reason is

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* R. G. Carruthers, 1908, Geol. Mag. pp. 20, 63, & 158.